

SYNOPSIS OF BIOLOGICAL DATA ON THE WHITE SHRIMP
Penaeus setiferus (Linnaeus) 1767

Exposé synoptique sur la biologie de
Penaeus setiferus (Linnaeus) 1767

Sínpesis sobre la biología del
Penaeus setiferus (Linnaeus) 1767

prepared by

MILTON J. LINDNER and HARRY L. COOK
Bureau of Commercial Fisheries
Biological Laboratory
Galveston, Texas 77550, U.S.A.

CONTENTS ^{1/}

	<u>Page No.</u>
1 IDENTITY	1:1
1.1 <u>Nomenclature</u>	1
1.11 Valid name	1
1.12 Objective synonymy	1
1.2 <u>Taxonomy</u>	1
1.21 Affinities	1
1.22 Taxonomic status	2
1.23 Subspecies	2
1.24 Standard common names, vernacular names	2
1.3 <u>Morphology</u>	2
1.31 External morphology	2
1.32 Cyto-morphology *	
1.33 Protein specificity	2
2 DISTRIBUTION	2:1
2.1 <u>Total area</u>	1
2.2 <u>Differential distribution</u>	1
2.21 Spawn, larvae and juveniles	1
2.22 Adults	1
2.3 <u>Determinants of distribution changes</u>	1
2.4 <u>Hybridization*</u>	
3 BIONOMICS AND LIFE HISTORY	3:1
3.1 <u>Reproduction</u>	1
3.11 Sexuality	1
3.12 Maturity	1
3.13 Mating	1
3.14 Fertilization	1
3.15 Gonads	1
3.16 Spawning	2
3.17 Spawn	2
3.2 <u>Pre-adult phase</u>	2
3.21 Embryonic phase	2
3.22 Larval phase	3
3.23 Adolescent phase	3
3.3 <u>Adult phase</u>	4
3.31 Longevity	4
3.32 Hardiness	5
3.33 Competitors	5
3.34 Predators	5
3.35 Parasites, diseases, injuries and abnormalities	6

^{1/} This synopsis has been prepared according to Outline Version No. 2
(H. Rosa Jr., FAO Fish. Synops., (1) Rev.1, 1965).

3.4	<u>Nutrition and growth</u>	3:6
3.41	Feeding	6
3.42	Food	6
3.43	Growth rate	7
3.44	Metabolism	7
3.5	<u>Behaviour</u>	7
3.51	Migrations and local movements	7
3.52	Schooling	9
3.53	Responses to stimuli	9
4	POPULATION	4:1
4.1	<u>Structure</u>	1
4.11	Sex ratio	1
4.12	Age composition	1
4.13	Size composition	1
4.2	<u>Abundance and density of population</u>	1
4.21	Average abundance *	
4.22	Changes in abundance	1
4.23	Average density	1
4.24	Changes in density	1
4.3	<u>Natality and recruitment</u>	2
4.31	Reproduction rates *	
4.32	Factors affecting reproduction *	
4.33	Recruitment	2
4.4	<u>Mortality and morbidity</u>	2
4.41	Mortality rates	2
4.42	Factors causing or affecting mortality	2
4.43	Factors affecting morbidity	2
4.44	Relation of morbidity to mortality rates *	2
4.5	<u>Dynamics of population (as a whole) *</u>	
4.6	<u>The population in the community and the ecosystem</u>	2
5	EXPLOITATION	5:1
5.1	<u>Fishing equipment</u>	1
5.11	Gears	1
5.12	Boats	1
5.2	<u>Fishing areas</u>	1
5.21	General geographic distribution	1
5.22	Geographic ranges	1
5.23	Depth ranges	1
5.24	Conditions of the grounds	1
5.3	<u>Fishing seasons</u>	1
5.31	General pattern of season(s) *	
5.32	Dates of beginning, peak and end of season(s) *	
5.33	Variation in date or duration of season *	

	<u>Page No.</u>
5.4 <u>Fishing operations and results</u>	5:1
5.41 Effort and intensity	1
5.42 Selectivity	3
5.43 Catches	3
6 PROTECTION AND MANAGEMENT	6:1
6.1 <u>Regulatory (legislative) measures</u>	1
6.11 Limitation or reduction of total catch *	
6.12 Protection of portions of population *	
6.2 <u>Control or alteration of physical features of the environment</u>	1
6.21 Regulation of flow *	
6.22 Control of water levels *	
6.23 Control of erosion and silting *	
6.24 Fishways at artificial and natural obstructions *	
6.25 Fish screens *	
6.26 Improvement of spawning grounds *	
6.27 Habitat improvement *	
6.3 <u>Control or alteration of chemical features of the environment *</u>	
6.31 Water pollution control	
6.32 Salinity control	
6.33 Artificial fertilization of waters	
6.4 <u>Control or alterations of the biological features of the environment *</u>	
6.41 Control of aquatic vegetation	
6.42 Introduction of fish foods (plant, invertebrate, forage fishes)	
6.43 Control of parasites and disease	
6.44 Control of predation and competition	
6.45 Population manipulation	
6.5 <u>Artificial stocking *</u>	
6.51 Maintenance stocking	
6.52 Transplantation; introduction	
7 POND FISH CULTURE	7:1
8 REFERENCES	8:1

* As no information was available to the author, these items have been omitted from the text.

1 IDENTITY

Definition

1.1 Nomenclature

1.11 Valid name

Penaeus setiferus (Linnaeus) 1767, Syst. Nat. (ed. 12) 1:1054

The controversy over the use of the name *setiferus* for the present species or for *P. schmitti* has been definitely decided in favor of the first alternative by the International Commission on Zoological Nomenclature in their Opinion 817 (1967, Bull. zool. Nomencl. 24(3):151).

1.12 Objective synonymy 1/

Astacus fluviatilis, *Americanus*, Seba, 1759

Cancer setiferus Linnaeus, 1767

Astacus setiferus (Linnaeus) Olivier 1791

Cancer (Gammarellus) setiferus (Linnaeus) Herbst, 1793

Penaeus fluviatilis Say, 1818 (an objective synonym of *Cancer setiferus* L., 1767, through the type selection by Holthuis, 1964, Bull. zool. Nomencl. 21(3):233).

Penaeus setifer (Linnaeus) L. Agassiz, 1849

1.2 Taxonomy

1.21 Affinities

Suprageneric (to family after Waterman and Chace, 1960)

Phylum Arthropoda
Class Crustacea
Subclass Malacostraca
Series Eumalacostraca
Superorder Eucarida
Order Decapoda
Suborder Natantia
Section Penaeidea
Family Penaeidae
Subfamily Penaeinae

Generic

Genus *Penaeus* Fabricius, 1798, Suppl. Ent. Syst. 385, 408. Type species, by selection by Latreille, 1810, Consid. gén. Anim. Crust. Arachn. Ins. 102, 422: *Penaeus monodon* Fabricius, 1798, Suppl. Ent. Syst. 408. Gender: masculine.

Rostrum toothed dorsally and ventrally. Carapace without longitudinal or transverse sutures; cervical and orbito-antennal sulci and antennal carinae always present. Hepatic and antennal spines pronounced, pterygostomial angle rounded. Telson with deep median sulcus, without fixed subapical spines, with or without lateral movable spines. First antennular segment without a spine on ventral distomedian border. Antennular flagella shorter than carapace. Maxillular palp with 2 or 3 segments, usually 3. Basal spines on 1st and 2nd pereopods; exopods on 1st 4 pereopods, usually present on 5th. Petasma symmetrical, pod-like with thin median lobes with or without distal protuberances; lateral lobes often with thickened ventral margin. Appendix masculina with distal segment subtriangular or ovoid, bearing numerous spines. Thelycum usually with an anterior process, variable in shape, lying between the coxae of 4th pereopods; with or without lateral plates on sternite XIV. Pleurobranchiae on somites IX to XIV: a rudimentary arthrobranch on somite VII, and a posterior arthrobranch on somite XIII; mastigobranchiae on somites VII to XII. Zygocardiac ossicle consisting of a principal tooth followed by a longitudinal row of smaller teeth which often end in a cluster of minute teeth. Body glabrous. (After Dall, 1957, slightly modified by Pérez-Farfante).

Specific

Identity of type specimens

The specimen figured by Seba (1759, Locuplet. Rer. nat. Thes. 3: pl. 17 fig. 2) is the holotype, or if the original description was based on more material, the lectotype of *Cancer setiferus* L. (by the selection by Holthuis, 1962, Gulf Research Rep. 1(3):115). The original type material is lost and a neotype has been designated by Burkenroad (1939, Bull. Bingham oceanogr. Coll. 6(6):17). The neotype is a male from Matanzas Inlet, Florida (0-10 fathoms, otter-trawl 2 April 1934, M.B. Bishop) in the Bingham Oceanographic Collection of Yale University, New Haven, Conn. U.S.A., preserved under no. B.O.C. 237. This neotype selection has been validated by the International Commission on Zoological Nomenclature in their Opinion 817 (1967, Bull. zool. Nomencl. 24(3):151).

Type locality

"In Indiis" (Linnaeus, 1767), restricted to "America" (Seba, 1759) by the lectotype selection (Holthuis, 1962) and still further restricted to Matanzas Inlet, Florida, U.S.A. by the neotype selection (Burkenroad, 1939).

1/ The authors wish to express their appreciation to Dr. Holthuis who provided the information in this section.

1.2

Diagnosis

Adrostral carina not reaching behind middle of carapace; gastrofrontal carina absent; hepatic carina present; rostral teeth usually 9 dorsal, 2 ventral; anterior portion of the ventral margin of the pleuron on the 1st pleonic somite almost straight; thelycum of female with open seminal receptacle; posterior portion of 14th sternite of female with conspicuous pair of fleshy protuberances; distoventral lobule of distomedian lobe of petasma rounded and not projecting; petasma of male with diagonal ridge across ventral face of distoventral lobe (Burkenroad, 1934, 1936; Ewald, 1965).

Subjective synonymy

Penaeus orbignyanus Latreille, 1817
(see Burkenroad, 1939, p.19).

Penaeus gracilirostris Thallwitz, 1891
(see Burkenroad, 1939, p.17).

Key to species

For key to species of the western Atlantic see section 1.21 of synopsis on *Penaeus schmitti* by Isabel Pérez-Farfante (1970).

1.22 Taxonomic status

Penaeus setiferus is one of the about 28 species of the genus *Penaeus*, and the first to ever get a valid scientific name. It is very close to *Penaeus schmitti* Burkenroad (see Species Synopsis 10) and was only distinguished from that species as late as 1936.

1.23 Subspecies

No subspecies are currently recognized in this species.

1.24 Standard common names

U.S.A.: white shrimp
Mexico: camarón blanco

Vernacular names

U.S.A.: common shrimp, archaic
green shrimp (Southport, N.Carolina)
" " (Jacksonville, Florida)
gray shrimp (N.Carolina and Florida)
green-tailed shrimp (Pamlico Sound,
N.Carolina)
blue-tailed shrimp (Ocracoke,
N.Carolina)
lake shrimp (Louisiana)

1.3 Morphology

1.31 External morphology

Young (1959) described in detail the skeletal and muscle systems and discussed the nervous, circulatory, digestive, excretory, and reproductive systems. Burkenroad (1934, 1939), Rioja (1939, 1940, 1941), and King (1948) described minute details of the external and internal reproductive systems.

Williams (1965, p.18) described the color "Body translucent, bluish white with dusky bands and patches composed of scattered black specks; rostrum and sides tinged with pink; blades of pleopods marked with dark red; antennae dark brown; uropods with tips of blades dark brownish purple with narrow stripe of yellowish green along margin."

Burkenroad (1934) reported that specimens from the Atlantic coast of the United States have longer rostrums than those from the Gulf of Mexico, but Lindner and Anderson (1956) believed Burkenroad was comparing immature Atlantic specimens with mature Gulf shrimp. Pérez-Farfante (personal communication) detected no differences between the Atlantic and Gulf of Mexico populations.

Mature shrimp have a shorter rostrum than immature shrimp of the same total length. Lindner and Anderson (1956, Fig.30) showed the relation between rostral length and total length for immature and mature female shrimp from Louisiana.

The bodies of older shrimp tend to thicken, and their weights are greater in proportion to length than are those of younger shrimp (Anderson and Lindner, 1958; Vioca, 1920).

(See also 3.11)

1.33 Protein specificity

Serological comparisons of saline-hemocyanin filtrates of *P. setiferus*, *P. aztecus* and *P. duorarum* from North Carolina by Leone and Pryor (1952, p.31) "... place *P. aztecus* and *P. duorarum* closer to each other than either is to *P. setiferus* ..." and "*P. setiferus* is more similar to *P. duorarum* than it is to *P. aztecus*." These authors also stated, "The serological differences are significant, and support the theory that these organisms are three distinct, but closely related, species".

2 DISTRIBUTION

2.1 Total area

According to Pérez-Farfante (personal communication), *P. setiferus* is limited to the east coast of the United States and the Gulf of Mexico, land areas 235, 237, 238, and 311 of FAO distribution code (Holthuis and Rosa, 1965). It has been reported from Fire Island, New York (Burkenroad, 1939), south to St. Lucie Inlet, Florida (Gunter, 1963), with the center of abundance off Georgia and north-eastern Florida. It was generally thought to be absent between St. Lucie Inlet and Ochlocknee River, Florida (Joyce and Eldred, 1966), but Springer and Bullis (1952), recorded one specimen from about 46 m of water at lat. 24°46' N, and long. 82°59' W. From Apalachicola Bay, Florida, a concentration extending westerly and southerly to northeastern Mexico has a center of abundance in Louisiana. A third concentration in the southern part of the Gulf of Campeche extends northeasterly along the coast from about Tupilco, Tabasco to Campeche, Campeche (Lindner, unpublished records). Bullis and Thompson (1965) caught *P. setiferus* at lat. 20°17' N, long. 91°35' W, which appears to be near the limit of its occurrence in this area. The greatest depth recorded for *P. setiferus* is about 82 m in the Gulf of Mexico near the mouth of the Mississippi River (Bullis and Thompson, 1965, OREGON station 1495, lat. 28°48' N, long. 89°26' W; 45 fm (82 m)).

The species is most abundant in areas characterized by extensive inland, brackish marshes connected by passes to shallow, off-shore areas of relatively high salinity and mud or clay bottoms (Anderson, King and Lindner, 1949). In the bays and shallow waters along the coasts of Georgia and the northwestern Gulf of Mexico, it is most frequently taken by otter trawls in association with fishes of the Family Sciaenidae (Anderson, personal communication; Gunter, 1945).

2.2 Differential distribution

2.21 Spawn, larvae, and juveniles

Most, and possibly all, spawning of *P. setiferus* is at sea. Off Louisiana, spawning probably does not occur in depths less than about 9 m (Pearson, 1939; Lindner and Anderson, 1956). At Port Aransas, Texas, Heegaard (1953, p. 78) believe it "spawns immediately outside the coast at a distance of 5 to 6 miles (9.3 to 11.1 km) from shore." Some spawning along a portion of the Atlantic coast may occur near shore. Pearson (1939) collected eggs on 5 occasions at St. Augustine Inlet, Florida, and Lindner and Anderson (1956, p. 616) on the basis of ripe shrimp taken in trawls stated, "... most spawning in Georgia and northern Florida is in outside

waters more than 1 mile (1.9 km) from shore, although some spawning may actually occur in inside waters in this area."

Off Louisiana, most spawning was in depths between 9 and 31 m (Lindner and Anderson, 1956). The greatest depth at which Pearson (1939) encountered larvae was about 55 m.

The eggs are demersal and the larval stages planktonic. Occasionally, eggs and larvae are carried into the estuaries (Pearson, 1939), but normally the young shrimp enter the estuarine nurseries as postlarvae at a total length (tip of rostrum to tip of telson) of 6 to 7 mm (Weymouth, Lindner and Anderson, 1933; Pearson, 1939; Anderson, King and Lindner, 1949; Bearden, 1961; Baxter and Renfro, 1966). On reaching the estuaries, the post-larvae become benthic (Anderson, Lindner and King, 1949; Williams, 1955). Habitats are characterized by shallow water, muddy or peaty bottoms high in organic detritus, abundance marsh grasses, moderate to low salinities, and widely fluctuating temperatures (Weymouth, Lindner and Anderson, 1933; Anderson, King and Lindner, 1949; Williams, 1955, 1955a; Loesch, 1965; Mock, MS).

As the shrimp grow, they move gradually from the shallow marginal areas to the deeper parts of the estuaries and then out to the open sea. They first appear on the estuarine fishing grounds in June or July, depending on locality, at a modal size of between 80 and 100 mm total length. Minimum length is about 50 mm (Weymouth, Lindner and Anderson, 1933; Gunter, 1950; Lindner and Anderson, 1956). Usually within a month of their appearance on the estuarine fishing grounds, some of the young have reached the open sea at a modal length of between 100 and 120 mm. This seaward movement continues throughout summer and is heightened in fall and winter by lowering temperatures (Lindner and Anderson, 1956).

2.22 Adults

See sections 2.1, 3.51, and 5.31.

2.3 Determinants of distribution changes

The determinants of distribution changes are largely unknown. Generally, it is presumed that postlarvae enter estuaries for food and shelter. Lindner and Anderson (1956) speculated that the movement from estuarine areas to the open sea was associated with approaching maturity. They and Gunter (1950) agree that this movement is intensified by falling temperatures during the latter part of the year.

Migrations along the Atlantic coast and offshore-onshore movements in the northern Gulf of Mexico during fall and winter were attributed to temperature changes by Lindner and Anderson (1956).

3 BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.11 Sexuality

Heterosexual. Sexes are easily distinguished: male with endopod of the 1st pair of pleopods modified to form a copulatory organ, the petasma; female with open type thelycum situated between the 3rd, 4th and 5th pereopods.

Rioja (1939, 1940) described the internal or medial antennular flagellum of adult males as being thicker and more robust than that of adult females; and having 16 of its segments each bearing 1 uniformly-large central and 2 small lateral spines. The lateral spines are lacking on some of the segments however, especially on the distal ones. The spines are absent in females, which have a tuft of bristles near the base of the external border much longer than in males. Rioja (1939) believed this antennular organ of the males to be sensorial and intimately related with sexual functions.

Four male white shrimp (143 to 180 mm total length) from the Texas coast that were examined by us differed from Rioja's description, which presumably was based on shrimp from the Gulf of Campeche. Three of the shrimp had 26 of their antennular segments bearing a large central spine, and the 4th had 24. There was only 1 lateral spine per segment and not all segments with large central spines had lateral spines. The number varied from 12 to 17. Dall (1957) said in his description of the genus Penaeus that the 3rd maxilliped is sexually dimorphic. Rioja (1948) who studied in detail the 3rd maxilliped of P. californiensis Holmes, P. stylirostris Stimpson, P. vannamei Boone, and P. setiferus, stated that the 3rd maxilliped of P. californiensis was sexually dimorphic. He did not describe, however, sexual dimorphism in the other species. From this statement we conclude that Rioja found no difference between the 3rd maxilliped of P. setiferus males and females. We examined 2 females (150 and 191 mm total length) and 1 male (163 mm) from the northwestern Gulf of Mexico and could find no sex-linked differences between proportions of each segment of the 3rd maxilliped against dactylus or between the total length of the shrimp against length of 3rd maxilliped. In all 3 specimens, the 3rd maxilliped extended to the distolateral edge of the antennular peduncle.

Weymouth, Lindner and Anderson (1933) noted a difference which increased with age in mean total lengths of the sexes. This disparity was later studied by Williams (1955) who concluded that after the mean size of the

shrimp in the population exceeded 100 mm, the mean total lengths of the females were consistently larger than those of the males.

3.12 Maturity

Broad (1965), interpreting length-frequency plots of Louisiana white shrimp published by Lindner and Anderson (1956), determined that sexual maturity is reached at a total length of 140 mm. Burkenroad (1934) reported that females become sexually mature at a carapace length of about 35 mm (about 165 mm total length) and that ripe sperm first appear at 25 mm carapace length (about 119 mm total length).

Distinctive changes in color and size accompany maturation of the ovary (King, 1948). Using these changes, King differentiated the following phases of development which are easily identified in the field.

Undeveloped: ovary small and transparent.

Developing: ovary opaque; scattered melanophores over the surface.

Yellow: ovary yellow to yellow-orange.

Ripe: ovary drab, olive-brown colored; very distended.

Recently spent: ovary collapsed and not as deeply colored as when ripe.

3.13 Mating

There is no record that mating has been observed, but it is believed that P. setiferus is promiscuous. The male attaches a spermatophore to the female before spawning. The spermatophore is placed externally between the 3rd, 4th, and 5th pairs of pereopods (King, 1948).

3.14 Fertilization

Generally believed to be external; upon emission, the eggs are fertilized by sperm from the spermatophore. Cook, however, (unpublished records) reported that recently captured gravid females, without external spermatophores, spawned viable eggs in the laboratory. These eggs hatched into apparently normal larvae which were reared to subadult size. The sex ratio of the juveniles was 1:1.

3.15 Gonads

No detailed investigations have been made on the relation of gonad size and number of eggs to body length, weight, or age. It has been estimated, however, that from 500,000 to 1,000,000 eggs are produced by one

individual at a spawning. Anderson, King and Lindner (1949) counted about 860,000 eggs in the ovaries of a ripe female 172 mm total length. Burkenroad (1934) reported that the spermatophores of large mature males were no larger than those from smaller mature males. King (1948), who examined the entire gonads of several specimens of both sexes, reported them to be homogenous in structure and stage of development of the germ cells.

3.16 Spawning

The number of times a white shrimp spawns in a single year is unknown. Most shrimp biologists agree that these shrimp may spawn repeatedly in a single season. Lindner and Anderson (1956) speculated that a single shrimp could spawn as many as 4 times in a season and indicated that a few females probably survived to spawn during a second season.

Weymouth et al. (1933, p. 24) stated that, "*P. setiferus* spawns from March or April to August or September" With considerably more data than those available to Weymouth et al., Lindner and Anderson (1956, p. 616) concluded, "When we consider sampling technique and errors, it appears probable that there is little, if any, difference between spawning seasons in any of the localities we covered between South Carolina and Texas. There probably is not more than about 2 weeks' difference in the beginning of spawning between any of the localities. Spawning may start later in South Carolina and Georgia than it does in Florida, Louisiana, and Texas, but in all the localities it probably begins either during the latter part of March or early in April and may possibly continue on into November, though probably it is completed by the end of September."

Lindner and Anderson (1956) placed the peak of spawning in June or July. More recent studies on ovarian development in the northwestern Gulf of Mexico by Renfro and Brusher (MS) and on occurrence of larvae in plankton collections by Temple and Fischer (1968) substantiate the findings of Lindner and Anderson (1956).

Spawning in laboratory aquariums has occurred only at night. On 2 occasions, *P. setiferus* spawned between 2230 and 2300 Central Standard Time (Cook, unpublished records).

Spawning is associated with size and probably also with age because the largest females spawn first (Weymouth et al., 1933; Lindner and Anderson, 1956).

Spawning also appears to be affected by temperature. Lindner and Anderson (1956, p. 620) stated, "Spawning in Louisiana appears

to be more closely associated with rising and falling temperatures than with absolute temperature. . . . The comparatively abrupt rise in the spring temperature coincides rather closely with the beginning of the spawning season and may, indeed, initiate it, while the season seems to terminate as soon as the temperatures begin to decline rapidly in the fall, even though they are at that time appreciably higher than those which evidently induced spawning in the spring."

Data from studies in areas where the 3 species *P. setiferus*, *P. duorarum* and *P. aztecus* occur together suggest that spawning seasons of the first 2 probably coincide. That of *P. aztecus* overlaps the others but its peak of spawning activity is either later or earlier (Williams, 1955; Joyce, 1965; Christmas, Gunter and Musgrave, 1966; Renfro and Brusher, MS). Temple and Fischer (1968) indicated that in the northwestern Gulf of Mexico peak spawning of *P. aztecus* occurs later than that of *P. setiferus* and that the larvae or postlarvae, or both, of *P. aztecus* overwinter in waters of the continental shelf.

The eggs are spawned directly into the water and there is no nesting or reproductive isolation.

Spawning activity within a season appears to increase to a single peak and then decline, but the young produced do not follow this pattern. Depending upon the locality, two or three broods of young shrimp may appear on the fishing grounds each season (Gunter, 1950; Lindner and Anderson, 1956).

3.17 Spawn

The eggs are demersal, nonadhesive and spherical. Live eggs measure 0.28 mm. Each egg has a thin, transparent membrane, or chorion, that gives a purplish-blue coloration in reflected light under the microscope (Pearson, 1939).

3.2 Pre-adult phase

3.21 Embryonic phase

In late developmental stages, the embryo is well-differentiated almost filling the egg, and leaving only a narrow perivitelline space. The length of the embryo is about 0.26 mm. The dark brown embryo is invested by a thin, transparent, and colorless embryonic membrane. Three pairs of appendages, corresponding to the 1st and 2nd antennae and mandibles, can be seen folded closely to the body. Several hours before hatching the embryo makes convulsive movements within the egg. The embryonic membrane is broken by the antennae. The egg membrane is normally ruptured soon after and the larva emerges. Actual emergence from the egg takes only a few seconds (Pearson, 1939).

3.22 Larval phase

White shrimp larvae were described by Pearson (1939) from specimens taken from the plankton. He encountered 5 naupliar sub-stages, 3 protozoal sub-stages, and 2 mysis sub-stages. Heegaard (1953) also reported 2 mysis sub-stages but an editorial footnote suggests more than 2. Three mysis sub-stages are present in laboratory-reared larvae (Cook, unpublished records). It is probable that Pearson did not encounter the 2nd mysis sub-stage.

Johnson and Fielding (1956) reported that the length of larval life was 10 to 12 days. They said, however, that the metamorphic period is not of fixed duration, but depends to some extent on local food and habitat. When reared in the laboratory at 30° C, larvae grew to 1st postlarvae in 9 to 13 days; those reared at 22° C required 15 to 24 days (Cook, unpublished records).

Nauplii do not feed, but utilize yolk granules which fill their body. Feeding starts at the 1st protozoal substage. In the laboratory, they are fed successfully with microscopic green algae and brine shrimp nauplii. First protozoa feed while swimming; movements of the maxillae and maxillipeds produce a feeding current (Pearson, 1939).

The sizes of the various larval stages are given in Table I.

3.23 Adolescent phase

During the early postlarval stages, the young shrimp are still planktonic in the offshore waters. At a total length of about 7 mm they enter the estuarine nursery grounds and take up a benthic existence, undergoing no striking morphological changes as they continue development. Williams (1953, 1959) has given characters which allow separation of certain size ranges of postlarval white shrimp from postlarval *P. aztecus* and *P. duorarum* of comparable size.

Various estimates have been made of growth during the adolescent phase. Viosca (1920) and Gunter (1950) estimated growth at about 1.0 mm per day; Williams (1955) at 1.2 mm per day; and Lindner and Anderson (1956) at 80 mm in 2 mo or 1.3 mm per day. Loesch (1965) suggested that "very young white shrimp may grow as much as 65 mm per month" or about 2.2 mm per day. Johnson and Fielding (1956) estimated that captive postlarvae grew at a rate of 2.1 mm per day for 24 days and 1.7 mm per day for the next 28 days. R. S. Wheeler (personal communication) grew postlarvae from 12.2 mm to 92.9 mm in 5 wk during the summer in a pond at Galveston, Texas; growth rate was 2.3 mm per day.

TABLE I
Size of egg, larvae and first postlarvae
of white shrimp (Pearson, 1939)

Stage of development	Length (mm)
Egg	0.28
Nauplius I	0.30-0.34
Nauplius II	0.32-0.34
Nauplius III	0.36-0.40
Nauplius IV	0.38-0.44
Nauplius V	0.46-0.56
Protozoa I	0.80-1.14
Protozoa II	1.3 -1.7
Protozoa III	2.2 -2.6
Mysis I	3.2 -3.8
Mysis II*	4.0 -4.4
Postlarva I	4.0 -5.0

* Probably Mysis III.

Williams (1955, 1955a), who studied estuarine habitats, noted that bottom areas of mud or fibrous peat are preferred by young *P. setiferus*, but that they occasionally occur on bottoms of sand or clay. He also concluded that the depth of water over these areas did not affect the numbers of shrimp, and that preferred areas usually had abundant cover, consisting primarily of organic litter and living vegetation. In controlled laboratory experiments, juvenile *P. setiferus* occurred more frequently on loose peat, sandy mud, and muddy sand than on shell sand and beach sand (Williams, 1958).

In Mobile Bay, Alabama, postlarval and juvenile *P. setiferus* (15 to 70 mm total length) were most abundant in water less than 0.6 m deep where the bottom contained large amounts of organic detritus (Loesch, 1965). Mook (MS), who sampled postlarval and juvenile white shrimp in an estuary at the shore and at a distance of about 15 m and 30 m from shore, encountered 98 percent of the white shrimp at the shore station. This shore area was characterized by an organic mat or peat bottom (composed of more than 40 percent organics) bordered by emergent vegetation that was under water at high tide.

Various investigators, including Gunter (1950, 1961), Gunter, Christmas and Killebrew (1964), Williams (1955a), and Joyce (1965) have reported that postlarvae and juveniles of *P. setiferus*, *P. aztecus*, and *P. duorarum* penetrate toward fresh water in the order given. Gunter, Christmas and Killebrew (1964) recorded lower salinity limits of 0.42‰ for *P. setiferus*, 0.80‰ for *P. aztecus* and 2.50‰ for *P. duorarum* in the northern Gulf of Mexico. On the northeast coast of Florida the lower salinity limits were: *P. setiferus*, 0.26‰; *P. aztecus*, 0.46‰; and *P. duorarum*, 0.64‰ (Joyce, 1965).

In Galveston Bay, Texas, Lee Trent and Jack Pullen (personal communication) on 23 April 1966, caught 9 *P. aztecus*, ranging in total length between 40 and 75 mm, in bottom salinity of 0.1‰. The bottom temperature was 28.0° C. On 12 July 1966 they captured 70 *P. setiferus*, 35 to 65 mm long, in a salinity of 0.7‰ and a temperature of 29.0° C. (There is some question as to the accuracy of the above low salinity records because they were determined from chlorinity analyses.)

At the other extreme, Gunter (1961) reported *P. setiferus* from a salinity of 41.3‰ and Hildebrand (1958) caught them, from 23 to 76 mm long, in Laguna Madre, Mexico in salinity of 47.96‰. Hildebrand (personal communication) stated: "In Laguna Madre of Texas, I have taken several specimens at a salinity of 62.4‰. However, this was in South Bay where the salinity might vary greatly with wind shifts and tidal patterns over relatively short periods of time. I also took it in salinities of 56.8‰ in the Upper Laguna Madre near South Bird Island. In general, I would agree with Simmons (1957) that it is generally rare at salinities greater than 40‰ and that the few that occur at higher salinities are strays or particularly hardy individuals which have survived a gradual increase in salinity."

In general, results of laboratory experiments substantiate field observations. Griffith and Zein-Eldin (personal communication) recorded 80 percent survival of *P. setiferus* after 1 mo's exposure to salinities of 4.0 and 54.0‰. These specimens were between 50 and 100 mm total length; they were held at a constant temperature of 25° C and were gradually acclimated to the final salinities over a period of 4 wk.

In another experiment, when shrimp increased in average total length from 6 to 50 mm in 28 days, 80 percent of the experimental population survived salinities of 2.0 and 40.0‰. Temperatures were held constant at 25° C and the acclimation period was 48 h.

Zoula Zein-Eldin and George Griffith (personal communication) believe that the period of acclimation is extremely important in determining the extremes of salinity and temperature at which *Penaeus* spp. can survive.

Temperature extremes are not documented as well as salinity extremes. Weymouth et al. (1933) encountered *P. setiferus* in temperatures ranging from 9° to 31° C. Both *P. setiferus* and *P. aztecus* have survived a temperature of 36° C in a pond in North Carolina (Lunz, 1956). The total length ranged between 5.1 and 9.5 cm for *P. setiferus* and between 11.4 and 17.8 cm for *P. aztecus*. The same author (1958) stated that shrimp (presumably *P. setiferus*) in ponds survived temperatures exceeding 38° C.

Trent and Pullen (personal communication), after examining data from studies in Galveston Bay, reported the catch of 1 live but immobile *P. setiferus* (65 mm total length) on 28 January 1963, where bottom temperature was 2.6° C and salinity 12.8‰. Their records also show a catch of 531 *P. setiferus* (mean total length 85 mm) at bottom temperature and salinity of 35.5° C and 24.0‰ on 26 August 1963.

Rapidly decreasing temperature is known to kill *P. setiferus*. The rapidity of the change appears to be more important than the actual temperature (Gunter, 1941; Gunter and Hildebrand, 1951; Lindner and Anderson, 1956; Lunz, 1958). Lethal temperatures are not known but Gunter (1941) reported surface water in Copano Bay, Texas, to have reached a low of 4° C during the 1940 kill and Lunz (1958) mentioned 4.5° C.

Weymouth et al. (1933) and Gunter (1950) obtained a positive correlation between salinity and size of white shrimp, but Lindner and Anderson (1956) demonstrated that the size relation was with locality rather than salinity.

Gunter and Hildebrand developed a relation between Texas rainfall and Texas catch of *P. setiferus*. The highest correlation was between the catch of the year and the average annual rainfall of that year and the two previous years, with high catches associated with high rainfall values. They believed this relation was caused by salinity changes in the bays (Hildebrand and Gunter, 1953; Gunter and Hildebrand, 1954).

3.3 Adult phase

3.31 Longevity

No method has been developed to determine reliably the age of an individual shrimp. Lindner (1953) developed a technique for estimating age for restricted periods by mark-recapture experiments, and Lindner and Anderson (1956)

demonstrated its usefulness in interpreting length-frequency distributions. Neither this technique, however, nor the von Bertalanffy growth formula, $L_t = L_{\infty} (1 - e^{-K(t-t_0)})$, can be used as a reliable indicator of shrimp age when the constant K changes as it does in *P. setiferus* between warm and cold periods. The method of Ursin (1963) may be an alternative.

Using information gained from maturity studies and length frequency plots, Lindner and Anderson (1956) demonstrated that *P. setiferus* lives at least 16 mo, but owing to high mortality, the number that live 2 yr or more is small with respect to the total population.

3.32 Hardiness

According to de Sylva (1954), *P. setiferus* is the least hardy, *P. aztecus* is the most hardy, and *P. duorarum* is intermediate. Field observations by the senior author while trawling, confirmed by David Harrington (personal communication), indicate *P. duorarum* to be the most hardy of the 3 species and *P. setiferus* the least. Butler (1962) observed that under laboratory conditions *P. aztecus* is more hardy than *P. setiferus*.

On the basis of size distribution in winter, Lindner and Anderson (1956) believed that juvenile and subadult *P. setiferus* are better able to withstand cold than the adults. Confirmation of this relation by experimental evidence is lacking.

Shrimp are extremely vulnerable to agricultural pesticides (Chin and Allen, 1957; Butler, 1962, 1963, 1966; Butler and Springer, 1963). Postlarval and small shrimp are generally more sensitive to pesticides than large shrimp; large white shrimp are less tolerant to some pesticides than large brown shrimp (Butler, 1962). Butler and Springer (1963, pp. 380, 381) stated, "Because shrimp, crabs, and other crustaceans are arthropods, like the insects, they understandably are sensitive to many of the chemical insecticides. Concentrations of heptachlor, endrin, and lindane in the range of 0.3-0.4 p.p.b. killed or immobilized half of the adult commercial brown and pink shrimp exposed in 48-h laboratory tests. Other chlorinated hydrocarbons, including DDT, chlordane, toxaphene, and dieldrin, showed similar effects at 1-6 p.p.b. In the laboratory, paralyzed individuals may live for days or even weeks, but in the struggle for survival in the sea this condition results almost immediately in death."

3.33 Competitors

Little is known about the competition among the 3 species of *Penaeus*. *P. setiferus* and *P. aztecus* may be competitors during most or all of their lives (Broad, 1965). Where the

3 species occur off Galveston, Texas, however, the adults occupy quite distinct areas. Adult *P. setiferus* are most abundant on mud or sandy mud bottoms shoreward of 27 m, and adult *P. aztecus* are on similar bottoms seaward of 27 m. Adult *P. duorarum* occur most abundantly on shell or sandy shell bottoms.

On the Galveston Bay nursery grounds, the bulk of *P. aztecus* young are leaving or have left these grounds before most postlarval *P. duorarum* and *P. setiferus* have arrived. When the postlarvae occur together on the same nursery grounds, those of *P. setiferus* are closer to shore than those of *P. aztecus* (Loesch, 1965; Mook, MS). Postlarvae of *P. duorarum* seem to prefer grass flats. Williams (1955a) reported seasonal, size, and areal differences in the estuarine distribution of postlarvae and juveniles of the 3 species in North Carolina.

3.34 Predators

No exhaustive study of white shrimp predators has been undertaken. Predators on larvae, undoubtedly numerous, are unknown. Robert Temple (personal communication) has observed *Penaeus* mysis in the digestive tracts of arrow worms (Chaetognatha), but he was unable to determine whether the arrow worms had been feeding on the larval shrimp or whether they had accidentally ingested the larvae while in the plankton net or while dying from the preservative.

Knapp (1949) examined 10,016 stomachs of 34 species of fishes from coastal waters of Texas between 7 June and 31 August 1948. Shrimp, principally *P. aztecus*, occurred in 61.8 percent of the 5,946 stomachs containing food. He reported shrimp as being the most widely used food between June and August, the season when *P. aztecus* is at peak biomass (Kutkuhn, 1962).

The following fish predators of *Penaeus* shrimp have been reported from the United States (areas 235 and 238 by Gunter (1945), Knapp (1949), Darnell (1958):

<i>Carcharhinus leucas</i>	<i>Coryphaena hippurus</i>
<i>Dasyatis sabina</i>	<i>Bairdiella chrysura</i>
<i>Elops saurus</i>	<i>Cynoscion arenarius</i>
<i>Megalops atlanticus</i>	<i>Cynoscion nebulosus</i>
<i>Anchoa mitchilli</i>	<i>Micropogon undulatus</i>
<i>Bagre marinus</i>	<i>Menticirrhus</i> sp.
<i>Galeichthys felis</i>	<i>Pogonias cromis</i>
<i>Ictalurus furcatus</i>	<i>Sciaenops ocellata</i>
<i>Roccus mississippiensis</i>	<i>Scomberomorus cavalla</i>
<i>Lutjanus blackfordi</i>	<i>Scomberomorus maculatus</i>
<i>Pomatomus saltatrix</i>	<i>Istiophorus</i> (Makaira)
<i>Rachyentron canadum</i>	<i>Paralichthys lethostigma</i>
<i>Caranx hippos</i>	

We believe the above list of predators is

incomplete. To us, Gunter's (1957, p. 102) remarks seem entirely appropriate: "It is a general observation of everyone working with shrimp that they are eaten by almost everything that is large enough to eat them, all the time. They are eaten by everything that lives around, in, or above the sea, including the lowly jellyfish. They are not only eaten but they are preferred."

The defense reaction of *Penaeus* is a rapid flexing of the abdomen that causes the animal to dart backward. In large specimens the distance may be 1 m or more in less than 1 sec (observations of the authors).

3.35 Parasites, diseases, injuries, and abnormalities

The following parasites have been recorded from *P. setiferus*: Class Telosporidae: *Nematopsis penaeus* Sprague, 1954. Found in intestinal tract of host (Sprague, 1954); occurs as trophozoites, sporonts, and gametocysts (Kruse, 1959). Kruse (1959) reported 100 percent infection in Alligator Harbor and Apalachicola Bay, Florida. Shrimp have to be continually reinfected, or they lose the infections (Sprague, 1954; Kruse, 1959). Intestinal epithelium can be appreciably damaged (Sprague, 1954).

Class Cnidosporidae: *Thelohania penaei* Sprague, 1950. Found in reproductive organs of male and female (Sprague, 1950); occurs as spores and sporonts (Sprague, 1950). Viosca (1943) stated that in 1919 about 90 percent of *P. setiferus* in Louisiana were infected with a protozoan that destroyed their reproductive organs.

Class Cnidosporidae: *Thelohania* sp. Kruse, 1959. Found mainly in muscles, it also occurs in other organs as sporonts, pansporoblasts, and spores. Kruse (1959) recorded 10 percent infection in Alligator Harbor and Apalachicola, Florida, and considered this organism to be the cause of the "cotton" or "milk" condition in *P. setiferus*, *P. aztecus* and *P. duorarum*. "Cotton shrimp," for esthetic reasons, are not acceptable for marketing in the United States.

Class Trematoda: *Opecoeloides fimbriatus* (Linton, 1934). Hutton et al. (1959, p. 19) found this parasite "Encysted in the hepatopancreas, the gonads, in the soft tissues of the head, around the mouth, around the stomach and in the soft tissues under the exoskeleton." It occurs as metacercaria in *Penaeus*, adults in various species of fishes of the Family Sciaenidae (Kruse, 1959; Hutton et al., 1959). Hutton et al. (1959) found a single specimen in white shrimp from Apalachicola Bay, Florida. Kruse (1959), who worked in the same area, encountered it only in *P. duorarum*.

Class Cestoda: *Prochristianella penaei* Kruse (1959). Found by Kruse (1959) in "digestive gland and tissues surrounding digestive gland and stomach, blastocysts of larvae frequently penetrating wall of digestive gland." Plerocerci occur in *Penaeus*, adults in the ray *Dasyatis sabina* (Aldrich, 1965). Kruse (1959) stated that in the northeastern Gulf of Mexico 94.4 per cent of *P. setiferus* were infected with an average of 14.7 plerocerci. Aldrich (1965) reported 50 percent of the white shrimp in Galveston Bay, Texas, to be infected. Both incidence and intensity of infection increase with the size of the shrimp, up to a size of about 14 mm carapace length (Aldrich, 1965).

Class Cestoda: *Polypocephalus* sp. (= *Parataenia* sp.). Hutton (1964) listed this cestode as infecting *P. setiferus* as an intermediate host. He reported it to be present in numerous localities in Florida.

Class Nematoda: *Contracaecum* sp. Kruse (1959) found juveniles "In digestive gland and tissues surrounding digestive gland and stomach, not encysted." The same author reported 5.5 percent infection in Alligator Harbor and Apalachicola Bay, Florida, and an average of 4 parasites per shrimp. Hutton, Ball and Eldred (1962) encountered 15.5 percent infestation and as many as 22 parasites in one specimen.

Dawson (1957) found maturing *Balanus* on 4 white shrimp.

3.4 Nutrition and growth

3.41 Feeding

From observations on *Penaeus* feeding in aquariums, the senior author is convinced that they are selective and particulate feeders. Shrimp search through the sand grains with their pereopods and pass toward the mandibles only that which they choose. They appear to be particularly fond of polychaete worms.

3.42 Food

Studies on the food habits of shrimp have been hindered because their stomach contents are usually macerated and difficult to identify. Viosca (1920) and Weymouth et al. (1933) reported *P. setiferus* to be omnivorous. In reviewing the literature on the food of the 3 species of *Penaeus* of the United States, Darnell (1958) and Broad (1965) reached the same conclusion. Cannibalism in captive *P. setiferus* was observed by Weymouth et al. (1933). Williams (1955), in discussing the food of the 3 species in North Carolina estuaries, stated that stomachs usually were full during summer, full or half-filled during fall, and nearly always empty in winter.

3.43 Growth rate

Lindner and Anderson (1956) demonstrated, by means of mark-recapture experiments, that growth in *P. setiferus* along the coasts of the United States was much less when the temperature was below 20° C than when it was above. They developed Walford (1946) growth lines from successive 10-day intervals for the period of rapid growth. These data, converted to 30-day lines, had the following characteristics:

Males $Y = 45.8 + 0.7427 X$ $L_{\infty} = 178.0$ mm
 Females $Y = 56.4 + 0.7225 X$ $L_{\infty} = 203.0$ mm
 Combined $Y = 51.00 + 0.7322 X$ $L_{\infty} = 190.45$ mm

Klima (1963, and personal communication) calculated von Bertalanffy growth parameters from two mark-recapture experiments. For 7-day periods these parameters were:

	1963	(Personal communication)
t_0	-0.6	-0.2
L_{∞}	224 mm	214 mm
W_{∞}	87 g	75.1 g
K	0.06	0.09

3.44 Metabolism

Johnson and Fielding (1956) fed fresh fish to 2 groups of small white shrimp at a rate of 10 percent of their initial body weight per day. One group was held at 34‰ salinity and the other at 18.5‰ for 2 wk. Their results are summarized in the table given below.

P. setiferus are able to regulate total body fluid concentrations. Body fluids are hyperosmotic in brackish water and hyposmotic in hypersaline environments. Regulation appears to be more effective in low-salinity water. Also, the shrimp regulate the ionic concentration of Na, Cl, K, Ca and Mg in their serum (McFarland and Lee, 1963).

Love and Thompson (1966) studied the amino acid concentration in abdomens of *P. setiferus* and *P. aztecus*. The amino acids they found are shown in Table II. Nitrogen content did not vary seasonally in brown shrimp tails or offal, but certain amino acids did. Concentrations of a number of amino acids differed significantly between *P. aztecus* and *P. setiferus*, but the variation between analyses of *P. aztecus* on different dates indicates that the differences between species may not be truly significant.

In an earlier study, Jones, Moeller and Gersdorff (1925) reported tryptophane in the muscle of *P. setiferus*.

Boroughs, Chipman and Rice (1957, p. 82) stated that *P. setiferus* "accumulated strontium rapidly from sea water."

3.5 Behaviour

3.51 Migrations and local movements

The young shrimp are planktonic in the offshore waters during their larval life and enter the estuaries as postlarvae about 7 mm total length. It is generally believed that these younger stages are not capable of extensive movement and that to reach the inside waters they must encounter favorable currents. Once in the estuaries, they make their way to the less saline, shallower areas, presumably by utilizing tidal currents. After growing rapidly for 3 or 4 mo, the young move into the deeper waters of the rivers and bays and then to sea. Movement out of the estuaries appears to depend on stage of maturity and temperature.

Lindner and Anderson (1956) described the general migration of adult white shrimp from shrimp tagged with Petersen discs. Klima (1963) reported on 2 experiments in Louisiana in which biological stains were used to mark white shrimp and found the same pattern of movement as described by Lindner and Anderson for tagged shrimp in that area.

The following account of white shrimp migrations has been taken from Lindner and Anderson (1956). The longest migration recorded

Salinity ‰	Initial weight (g)	Terminal weight (g)	Gain (g)	Gain (%)	Food consumed (g)	Conversion ratio
34.0	32.7	37.3	4.6	14.1	19.2	4.09:1
18.5	29.4	32.7	3.3	11.2	17.4	5.27:1

TABLE II

Average amino acid concentrations in tail meats of Gulf of Mexico Shrimp
(adapted from Love and Thompson, 1966)

Amino acids	Average amino acid concentration			Significant species difference between samples taken on 20/2/64	
	<i>P. a. aztecus</i>				<i>P. setiferus</i> 20/2/64
	14/1/63	20/2/64	25/3/63		
	<u>μ moles/mg N</u>			<u>μ moles/mg N</u>	
Alanine	3.70	3.64	4.26	4.36	
Arginine	3.16	3.81	3.60	3.81	
Aspartic acid	3.98	4.14	4.64	5.57	*
Cystine/2	0.33	0.36	0.09	0.38	
Glutamic acid	4.90	4.97	5.64	6.22	*
Glycine	6.35	6.19	6.45	6.96	
Histidine	0.67	0.79	0.76	0.86	
Hydroxylysine	0.05	0.03	0.01	0.04	
Hydroxyproline	0.09	0.11	0.03	0.01	*
Isoleucine	1.86	2.02	2.13	2.59	*
Leucine	3.35	3.59	3.87	4.32	*
Lysine	2.82	3.52	3.11	3.46	
Methionine	0.87	1.04	1.06	1.25	
Ornithine	0.13	0.10	0.12	0.11	
Phenylalanine	1.11	1.20	1.30	1.42	
Proline	2.11	2.29	2.46	2.47	
Serine	1.92	1.96	2.33	2.40	*
Taurine	0.47	0.31	0.57	0.65	*
Threonine	1.70	1.77	1.93	2.16	*
Tryptophan	0.39	-	0.45	-	
Tyrosine	0.77	0.85	0.74	0.89	
Urea	0.07	0.08	0.16	-	
Valine	2.06	2.31	2.57	2.80	*

* Indicates difference

was 360 mi (667 km) in 95 days, and the greatest time between marking and recapture was 257 days.

After reaching outside waters, movements vary with size, locality, and season. Shrimp less than 130 mm, total length, did not migrate extensively, but remained adjacent to their nursery areas. Shrimp larger than 130 mm exhibited distinct migrations that varied with locality.

Atlantic coast: The white shrimp in this area migrate southward during the autumn and early winter and then move northward again in late winter and early spring. These movements parallel the coast, and do not extend into deeper water far from the coast. During late spring and summer movement is not pronounced.

Northern Gulf east of the Mississippi: All that is known of movement in this area is that during autumn and winter the shrimp move into deeper water and toward the mouth of the Mississippi River.

Northern Gulf west of the Mississippi River: The only definite movements in this area are offshore and onshore movements. The large shrimp move offshore and disperse during autumn and winter. Apparently the Mississippi River acts as a natural barrier.

Central Texas and northern Mexico: The migration in this part of the Gulf appears similar to that on the Atlantic coast, but the evidence is not conclusive. Indications are that the shrimp move from central Texas into northern Mexico during autumn and early winter.

There should also be a corresponding northward migration out of Mexico in the spring.

3.52 Schooling

Hildebrand (1954) stated that white shrimp school more extensively than related species.

The senior author believes that white shrimp of about the same age or length tend to aggregate in groups but that these aggregations do not possess the consistency through time generally attributed to a school of fish.

3.53 Responses to stimuli

Thermal

See section 3.16 for effect of temperature on spawning and 4.42 for lethal temperatures.

Lindner and Anderson (1956) found that *P. setiferus* moved from shallow to deeper water in response to unusual cold spells. They also uncovered evidence that the smaller shrimp moved back into shallower water as the water temperature increased.

Optical

Temple and Fischer (1965) demonstrated that penaeid larvae showed vertical diurnal migrations when the water column was vertically stable. Larvae moved into the surface layers in darkness and into deeper water during daylight.

4 POPULATION

4.1 Structure

4.11 Sex ratio

The sex ratio is 1:1.

4.12 Age composition

The mortality rate is high, and while some white shrimp may live more than 2 yr, the percentage is insignificant. Age composition of the catch consequently varies directly with recruitment and movement of the maturing shrimp into offshore waters.

The young enter the inshore fishery at an age of about 2 mo and the offshore fishery at about 3 or 4 mo.

4.13 Size composition

Size composition varies in the same manner as age composition.

The young enter the inshore fishery at a minimum total length of about 50 mm and the offshore fishery at a minimum total length of about 100 mm. Lindner and Anderson (1956) give an L_{50} of 203 mm for females and an L_{50} of 178 mm for males (see also 3.43).

The weights of large shrimp are greater in relation to length than are those of small ones. There is no appreciable difference in length-weight relations between sexes. Chin (1960) expressed the length-weight relation with the following equation:

$$\log W = -5.289 + (3.075) (\log L)$$

This equation agrees with the length-weight relation given by Anderson and Lindner (1958) until the shrimp reach a total length of 143 mm. Above this size, weights at comparable lengths given by Anderson and Lindner were greater than those of Chin (1960). Anderson and Lindner found a difference in length-weight relations between mature and immature shrimp; mature shrimp weighed more at a given total length. Chin believed that this factor might explain the differences between the 2 sets of data.

4.2 Abundance and density of population

4.22 Changes in abundance

White shrimp production peaked in the early 1940's. Production in 1940 is estimated to have been about 65,000 metric tons, whole weight. At this time, intensive fishing for brown and pink shrimp had not started, and white shrimp were estimated to account for 95 percent or more of the total catch (Anderson,

Lindner and King, 1949). Between 1945 and 1948, production of white shrimp declined and has not approached the high levels of the early 1940's since then. During the years for which we have reliable statistics (1957 to 1965, Table III), the catch has varied from 14,447 metric tons in 1957 to 36,188 in 1963. The cause of these fluctuations is not known.

TABLE III

United States white shrimp landings
in metric tons, whole weight

Year	East coast, North Carolina to Florida	Gulf coast, Florida to Texas	Total
1957	6,673	7,774	14,447
1958	5,032	17,980	23,012
1959	5,816	17,167	22,983
1960	8,522	19,826	28,348
1961	6,365	10,093	16,458
1962	5,504	16,181	21,685
1963	3,297	32,891	36,188
1964	3,683	30,720	34,403
1965	7,395	23,470	30,865

In 1940, the white shrimp population in South Carolina and Georgia was decimated by a severe cold spell. In 1941, the return of landings to normal indicated that a normal crop may be produced by relatively few spawners (Lindner and Anderson, 1956). Kutkuhn (1962) attributed the low 1957 landings of white shrimp in Louisiana to the effects of severe storms which struck the coast while the young of the spring spawning class were in the estuaries. Again, the fishery made a good recovery after 1 yr.

4.23 Average density

Kutkuhn (1962) indicated the 4-yr trend (1956 to 1959) in biomass of *P. setiferus* in the northern Gulf of Mexico to have been increasing to the east of the Mississippi River and decreasing to the west.

4.24 Changes in density

There are 2 periods of increased density on the offshore fishing grounds, one in late fall and the other in spring (Weymouth, et al., 1933; Lindner and Anderson, 1956; Kutkuhn, 1962).

4.3 Natality and recruitment

4.33 Recruitment

Rate of recruitment has not been determined. With some local variation, inshore recruitment starts in June and continues until the onset of cold weather (Lindner and Anderson, 1956).

4.4 Mortality and morbidity

4.41 Mortality rates

Klima (1963) gave an instantaneous total mortality rate of 0.92 for white shrimp off Louisiana from September through November. This is a 14-day rate of decline of 60 percent.

4.42 Factors causing or affecting mortality

See sections 3.34 and 4.22

4.43 Factors affecting morbidity

See sections 3.23, 3.32, and 3.35

4.6 The population in the community and the ecosystem

After making an extensive survey of macrofauna on the white shrimp grounds in the Gulf of Mexico, Hildebrand (1954) listed the dominant organisms to be: White shrimp, Penaeus setiferus; blue crab, Callinectes danae; sea pansy, Renilla mulleri; Texas venus, Pitar texasiana; silver seatrout, Cynoscion nothus; Atlantic croaker, Micropogon undulatus; Atlantic threadfin, Polydactylus otonemus; and sea catfish, Galeiothys felis.

5 EXPLOITATION

5.1 Fishing equipment

5.11 Gears

The various gears used in the inshore fishery for white shrimp range from the modern trawl to primitive weirs and include trynets, pushnets, frame trawls, lift or drop nets, side frame trawls, seines, cast nets and dip nets. In the United States some shrimp are taken in estuaries for sale as bait, largely with a single 3- to 11-m otter trawl with a stretched mesh size of 3 to 5 cm. If the shrimp are to be kept alive, they are placed in a tank on the boat equipped with running sea water, or in a live box which is towed behind the boat. On shore, the live shrimp are kept usually in large bait boxes suspended in the water or in large holding tanks through which sea water is pumped (Inglis and Chin, revised by Baxter, 1966).

Most vessels fishing in offshore waters use a pair of 12- to 15-m flat or balloon otter trawls, but some use only one. Almost all boats use trynets, which are miniature trawls, to locate fishable concentrations of shrimp. A detailed description of trawling gear was given by Robas (1959).

In the early fishery in the United States, fishing was primarily with haul seines and cast nets. In Mexico, fixed traps predominated. Between 1912 and 1915, the otter trawl was introduced and by 1917, it had become the standard commercial gear. Practically all shrimp boats on the Atlantic coast were equipped with power winches by the mid-twenties, but with the exception of Texas, winches were not introduced into the Gulf until the late thirties (Johnson and Lindner, 1934; Anderson, Lindner and King, 1949). In the Gulf of Mexico, double-rig trawling was tried first in 1955, and was soon adopted by most offshore boats (Knake, Murdock and Cating, 1958).

5.12 Boats

Vessels of varied design, usually not exceeding 9 to 14 m in length, are used in the inshore fishery. Power is supplied by engines that burn gasoline or distillate. The boats are equipped usually with power winches and rope or wire towlines (U.S. Fish and Wildlife Service, 1958).

Vessels in the offshore fishery are predominantly Florida-type trawlers, which are described in detail by Cook and Lindner (1970).

5.2 Fishing areas

5.21 General geographic distribution

P. setiferus is fished along the Atlantic coast from Pamlico Sound, North Carolina to about Vero Beach, Florida (land areas 237 and 238) and in the Gulf of Mexico from Apalachicola, Florida to about lat. 23° N on the Mexican coast (land areas 235, 237, and 311). Between lat. 23° N and Tupilco, Tabasco, Mexico, there is no fishery. From Tupilco, however, the fishery extends eastward to about Champoton, Campeche. The 3 centers of abundance are in Georgia, Louisiana, and between Alvaro Obregón, Tabasco, and Isla del Carmen, Campeche (Hildebrand, 1955; Carranza, 1959; Anderson and Lunz, 1965; and Lindner, personal observations).

5.22 Geographic ranges

The accompanying map (Fig. 1) adapted from Hildebrand (1954), Lindner and Anderson (1956), Anderson and Lunz (1965), and Lindner (personal observations), delineates the primary fishing areas.

5.23 Depth ranges

The white shrimp has been recorded from depths down to 82 m, but it is most abundant on bottoms shoreward of 27 m (see sections 2.1 and 3.33).

5.24 Condition of grounds

See section 2.1.

5.3 Fishing seasons

White shrimp are harvested all year but peak production is in the autumn. Between 1956 and 1959, the greatest monthly catch in Texas waters was taken in September, about 63 percent of the catch was made during September and October and about 84 percent from August through November. The only other month of high production was May (Gunter, 1962). The greatest catch off the east coast of Florida is made from September through January and the peak is in December (Joyce, 1965).

5.4 Fishing operations and results

5.41 Effort and intensity

Fishermen frequently land mixed catches of brown, white and pink shrimp. In these instances, effort is reported only for the dominant species and not by individual species. As a result, there have been no reliable studies that require effort information on individual species.

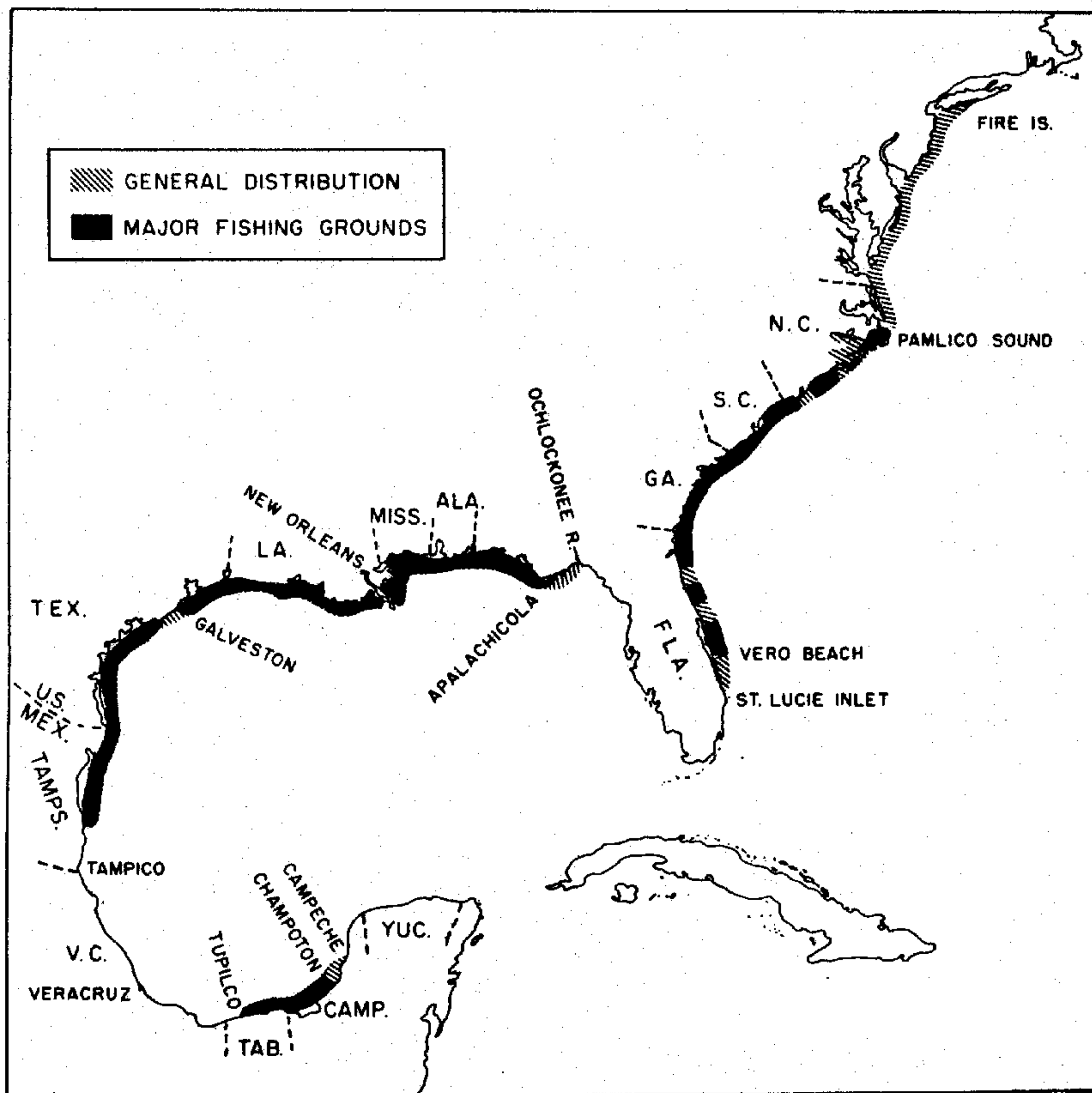


Fig. 1 Distribution and major fishing areas for *Penaeus setiferus*.

5.42 Selectivity

No critical data are available for P. setiferus on the selective properties of gear or effects of changes in mesh sizes but, presumably studies on the other 2 species would be applicable.

Market prices of all commercial penaeids in the United States are based on size; the largest shrimp command the highest price. Fishermen frequently fish in areas that yield larger shrimp in preference to areas with too many small shrimp. When large quantities of small shrimp are taken, it is not uncommon for them to be discarded either because they do not meet minimum size regulations, or because the fishermen do not want to bother with them.

Laws on minimum size are enacted by individual states and therefore vary.

Offshore shrimp fleets are highly mobile, and are moving continually from one location to another as abundance of the 3 commercially important species changes. During periods of

peak abundance of one species, boats frequently concentrate in relatively small areas, leaving other areas and species unfished. At other times of the year, the fleet is dispersed over the entire fishing range.

5.43 Catches

See section 4.22.

Table IV gives United States shrimp production through 1940. It is estimated that white shrimp constituted more than 95 percent of these landings. The United States began collecting more detailed statistics on its Gulf coast landings in 1956 and expanded this coverage to the Atlantic coast fishery in 1957. Table III (section 4.22) gives the United States white shrimp landings since 1957. These landings do not include production from the bait fisheries, which in some areas is substantial. During 1964, for example, more than 850,000 lb (about 400,000 kg) of shrimp were taken for bait in Galveston Bay, Texas (Inglis and Chin, revised by Baxter, 1966). About 65 percent or 250,000 kg were white shrimp (Kenneth Baxter, personal communication).

TABLE IV

United States shrimp landings through 1940
in metric tons, whole weight (Power, 1960)

Year	East coast, North Carolina to Florida	Gulf coast, Florida to Texas	Total
1889	337	3,767	4,104
1890	337	3,380	3,717
1897	284	3,081	3,365
1902	1,729	5,609	7,338
1908	2,584	5,835	8,419
1918	7,101	14,672	21,773
1923	10,761	21,371	32,132
1927	13,604	31,242	44,846
1928	15,109	37,271	52,380
1929	13,984	35,254	49,238
1930	11,886	28,083	39,969
1931	11,564	32,185	43,749
1932	10,189	29,846	40,035
1934	11,776	42,346	54,122
1936	15,226	38,348	53,574
1937	12,445	51,636	64,081
1938	12,503	51,068	63,571
1939	12,558	54,605	67,163
1940	10,297	57,986	68,283

6 PROTECTION AND MANAGEMENT

6.1 Regulatory (legislative) measures

In the U.S.A., each of the shrimp-producing States has its own legislation but all require licenses for fishing vessels. In Mexico, only members of legally authorized fishing cooperatives can fish commercially for shrimp (U.S. Fish and Wildlife Service, 1958; Lindner, 1957).

In the U.S.A., regulatory measures vary greatly between States and sometimes, even between counties within a State. The following types of regulatory measures are commonly imposed:

- (i) Limitations on size and type of gear used;
- (ii) limitations on size of shrimp permitted to be landed;

- (iii) limitations on catch in inside waters;
- (iv) permanent and temporary closure of inside waters;
- (v) temporary closure of outside waters within territorial limits.

6.2 Control or alterations of physical features of the environment

Mook (MS) demonstrated that the abundance of postlarval and juvenile shrimp is reduced greatly along bulkheaded portions of estuarine borders. He has also obtained data (personal communication) which show that silt from dredging and spoil banks kills submerged vegetation. Submerged vegetation is a preferred habitat of young Penaeus, and as the vegetation disappears from an area the number of shrimp decreases greatly.

7 POND FISH CULTURE

In general, *P. setiferus* is regarded as being well suited for pond culture. Attempts at culturing have been experimental, however, and there are no commercial pond culture operations at the present time.

In one of the earlier culture experiments conducted by Johnson and Fielding (1956), sexually mature *P. setiferus* that had been reared or held in dirt ponds spawned viable eggs when placed in a 21 x 9 x 12 m concrete tank filled with sea water. The resulting larvae were reared to postlarvae in 10 to 12 days. The shrimp were reared to a total length of 50 mm in the tanks in which they were hatched. Water in the tank was fertilized with a commercial inorganic fertilizer (7 parts elemental nitrogen; 9 parts phosphoric acid; 0 parts potash) to promote algal growth for larval food during early development. Later stages were fed daily on ground fish.

The work of Johnson and Fielding has not been repeated and subsequent workers have had to rely on postlarvae taken from the estuaries to stock their ponds. Recently, however, Cook (1969) developed a method for culturing white shrimp larvae under laboratory conditions. Although this method needs further modification before large-scale culture becomes practical, sufficient numbers of postlarvae were reared to stock a 0.05-ha (1/8-acre) pond. After the laboratory-reared shrimp had been in the pond 117 days, Ray Wheeler (personal communication) harvested 32 kg (70 lb) of shrimp with an

average total length of 112 mm. Survival was 84 percent. Wheeler did not add supplemental food; instead he fertilized the pond water with chicken manure. During the first 35 days, the shrimp grew at a rate of 2.33 mm per day, but during the remainder of the experiment average growth was reduced to only 0.23 mm per day.

Lunz (1967) reported that white shrimp stocked in ponds as young adults in the spring reached sexual maturity the following spring, but they did not spawn. Personnel at the Bears Bluff Laboratories, Wadmalaw Island, South Carolina, have also succeeded in rearing white shrimp postlarvae from eggs spawned in the laboratory. Lunz (1967) said that some eggs hatched and 2 percent of the resulting larvae were reared to postlarvae.

Johnson and Fielding (1956) were troubled by excessive mortalities, as have been subsequent workers. One of the causes of mortality has been the presence of predaceous fish. Lunz and Bearden (1963) found that rotenone, a specific poison for fish, does not kill shrimp and other decapod crustaceans when applied in proper concentrations. They used 1.4 kg (3 lb) of powdered cube root with a 5-percent-rotenone content for each 1,233 m³ of water, giving a rotenone concentration of about 1.5 parts per million. Saponin, a poison contained in tea seed cake, is used for fish control in Asia, but Lunz and Bearden (1963) found it to be too expensive for general use, even though it worked satisfactorily.

8 REFERENCES

- Agassiz, L., Twelve lectures on comparative embryology, delivered before the Lowell
1849 Institute, in Boston, December and January 1848-9. Redding and Co., Boston,
104 p.
- Aldrich, D.V., Observations on the ecology and life cycle of Prochristianella penaei
1965 Kruse (Cestoda: Trypanorhyncha). J.Parasit., 51(3):370-6
- Anderson, W.W. and M.J. Lindner, Length-weight relation in the common or white shrimp,
1958 Penaeus setiferus. Spec.scienc.Rep.U.S.Fish Wildl.Serv.(Fish.), (256):13 p.
- Anderson, W.W. and G.R. Lunz, Southern shrimp, a valuable regional resource. Leafl.
1965 Atlant.St.mar.Fish.Comm., (4):6 p.
- Anderson, W.W., J.E. King and M.J. Lindner, Early stages in the life history of the
1949 common marine shrimp, Penaeus setiferus (Linnaeus). Biol.Bull.mar.biol.lab.,
Woods Hole, 96(2):168-72
- Anderson, W.W., M.J. Lindner and J.E. King, The shrimp fishery of the southern United
1949 States. Comm.Fish.Rev., 11(2):1-17. Also issued as Fishery Leafl.U.S.Fish
Wildl.Serv., (368):17 p.
- Baxter, K.M. and W.C. Renfro, Seasonal occurrence and size distribution of postlarval
1966 brown and white shrimp near Galveston, Texas, with notes on species identi-
fication. Fishery Bull.U.S.Fish Wildl.Serv., 66(1):149-58
- Bearden, C.M., Notes on postlarvae of commercial shrimp (Penaeus) in South Carolina.
1961 Contr.Bears Bluff Labs., (33):8 p.
- Boroughs, H., W.A. Chipman and T.R. Rice, Laboratory experiments on the uptake accu-
1957 mulation and loss of radionuclides by marine organisms. In The effects of
atomic radiation on oceanography and fisheries. Publs natn.Res.Coun., Wash.,
(551):80-7
- Broad, A.C., Environmental requirements of shrimp. Publs publ.Hlth Serv., Wash., (999-
1965 WP-25):86-91
- Bullis, H.R., Jr. and J.R. Thompson, Collections by the fishing vessels OREGON, SILVER
1965 BAY, COMBAT and PELICAN made during 1956-1960 in the southwestern north
Atlantic. Spec.scienc.Rep.U.S.Fish Wildl.Serv.(Fish.), (510):130 p.
- Burkenroad, M.D., The Penaeidae of Louisiana with a discussion of their world relation-
1934 ships. Bull.Am.Mus.nat.Hist., 68(2):61-143
- _____, A new species of Penaeus from the American Atlantic. Anais Acad.bras.
1936 Cieno., 8(4):315-8
- _____, Further observations on Penaeidae of the northern Gulf of Mexico. Bull.
1939 Bingham oceanogr.Coll., 6(6):1-62
- Butler, P.A., Effects on commercial fisheries. In Effects of pesticides on fish and
1962 wildlife in 1960. Circ.Fish Wildl.Serv., Wash., (143):20-4
- _____, Commercial fisheries investigations. In Pesticide-wildlife studies, a
1963 review of Fish and Wildlife Service investigations during 1961 and 1962.
Circ.Fish Wildl.Serv., Wash., (167):11-25
- _____, Fixation of DDT in estuaries. Trans.N.Am.Wildl.Conf., 31:184-9
1966

- Butler, P.A. and P.F. Springer, Pesticides - a new factor in coastal environments.
1963 Trans.N.Am.Wildl.Conf., 28:378-90
- Carranza, J., Pesca y recursos pesqueros. In Los recursos naturales del sureste y su
1959 aprovechamiento, México, D.F., Instituto Mexicano de Recursos Naturales
Renovables, 3:149-238
- Chin, E., The bait shrimp fishery of Galveston Bay, Texas. Trans.Am.Fish.Soc., 89(2):
1960 135-41
- Chin, E. and D.M. Allen, Toxicity of an insecticide to two species of shrimp, Penaeus
1957 aztecus and Penaeus setiferus. Tex.J.Sci., 9(3):270-8
- Christmas, J.Y., G. Gunter and P. Musgrave, Studies of annual abundance of postlarval
1966 penaeid shrimp in the estuarine waters of Mississippi as related to subse-
quent commercial catches. Gulf Res.Rep., 2(2):177-212
- Cook, H.L., A method of rearing penaeid shrimp larvae for experimental studies. FAO
1969 Fish.Rep., (57) Vol.3:709-15
- Cook, H.L. and M.J. Lindner, Synopsis of biological data on the brown shrimp Penaeus
1970 aztecus aztecus Pérez-Farfante. FAO Fish.Rep., (57) Vol.4:1471-97
- Dall, W., A revision of the Australian species of Penaeinae (Crustacea Decapoda:
1957 Penaeidae). Aust.J.mar.Freshwat.Res., 8(2):136-231
- Darnell, R.M., Food habits of fishes and larger invertebrates of Lake Pontchartrain,
1958 Louisiana, an estuarine community. Publs.Inst.mar.Sci.Univ.Tex., 5:353-415
- Dawson, C.E., Balanus fouling of shrimp Penaeus. Science, N.Y., 126(3282):1068
1957
- De Sylva, D.P., The live bait shrimp fishery of the northeast coast of Florida. Tech.
1954 Ser.Fla.St.Bd Conserv., 11:35 p.
- Ewald, J.J., Investigaciones sobre la biología del camarón comercial en el occidente
1965 de Venezuela. Informe a.Fondo nac.Investnes agropec., Caracas, 2:139-47
- Gunter, G., Death of fishes due to cold on Texas coast, January, 1940. Ecology,
1941 22:203-8
- _____, Studies on marine fishes of Texas. Publs.Inst.mar.Sci.Univ.Tex., 1(1):
1945 1-190
- _____, Seasonal population changes and distributions as related to salinity, of
1950 certain invertebrates of the Texas coast including the commercial shrimp.
Publs.Inst.mar.Sci.Univ.Tex., 1(2):1-51
- _____, Principles of shrimp fishery management. Proc.Gulf Caribb.Fish.Inst.,
1957 8:99-106
- _____, Habitat of juvenile shrimp (Family Penaeidae). Ecology, 42:598-600
1961
- _____, Shrimp landings and production of the state of Texas for the period 1956-
1962 1959, with a comparison with other Gulf States. Publs Inst.mar.Sci.Univ.
Tex., 8:216-26
- _____, The proper zoological name of the North American white shrimp. Proc.
1963 Gulf Caribb.Fish.Inst., 15:103-10

- Gunter, G. and H.H. Hildebrand, Destruction of fishes and other organisms on the south
1951 Texas coast by the cold wave of January 28-February 3, 1951. Ecology, 32(4):
731-6
- _____, The relation of total rainfall of the state and catch of the marine
1954 shrimp (Penaeus setiferus) in Texas waters. Bull.mar.Sci.Gulf Caribb., 4(2):
95-103
- Gunter, G., J.Y. Christmas and R. Killebrew, Some relations of salinity to population
1964 distributions of motile estuarine organisms, with special reference to
penaeid shrimp. Ecology, 45(1):181-5
- Heegaard, P.E., Observations on spawning and larval history of the shrimp Penaeus
1953 setiferus (L.). Publs Inst.mar.Sci.Univ.Tex., 3(1):73-105
- Herbst, J.F.W., Versuch einer Naturgeschichte der Krabben und Krebse nebst einer system-
1793 atischen Beschreibung ihrer verschiedenen Arten. Berlin, Vol.2, 225 p.
- Hildebrand, H.H., A study of the fauna of the brown shrimp (Penaeus aztecus Ives)
1954 grounds in the western Gulf of Mexico. Publs Inst.mar.Sci.Univ.Tex., 3(2):
231-366
- _____, A study of the fauna of the pink shrimp (Penaeus duorarum Burkenroad)
1955 grounds in the Gulf of Campeche. Publs.Inst.mar.Sci.Univ.Tex., 4(1):
169-232
- _____, Estudios biológicos preliminares sobre la Laguna Madre de Tamaulipas.
1958 Ciencia, Méx., 17(7-9):151-73
- Hildebrand, H.H. and G. Gunter, Correlation of rainfall with the Texas catch of white
1953 shrimp, Penaeus setiferus (Linnaeus). Trans.Am.Fish.Soc., 82:151-5
- Holthuis, L.B., On the names of Penaeus setiferus (L.) and Penaeus schmitti Burkenroad.
1962 Gulf Res.Rep., 1(3):115-8
- _____, Cancer setiferus Linnaeus, 1767 (Crustacea, Decapoda): proposed valida-
1964 tion of neotype selection under the plenary powers Z.N.(S.) 1617. Bull.
zool.Nom., 21(3):227-9
- Holthuis, L.B. and H. Rosa, Jr., List of species of shrimps and prawns of economic
1965 value. FAO Fish.tech.Pap., (52):21 p.
- Hutton, R.F., A second list of parasites from marine and coastal animals of Florida.
1964 Trans.Am.microsc.Soc., 83(4):439-47
- Hutton, R.F., T. Ball and B. Eldred, Immature nematodes of the genus Contracaecum
1962 Railliet and Henry, 1912 from shrimps. J. Parasit., 48(2):327-32
- Hutton, R.F., et al., Investigations on the parasites and diseases of salt water
1959 shrimps (Penaeidae) of sports and commercial importance to Florida.
Tech.Ser.Fla St.Bd Conserv., 26:38 p.
- Inglis, A. and E. Chin, (revised by K.N. Baxter), The Bait shrimp industry of the
1966 Gulf of Mexico. Fishery Leaflet.U.S.Fish Wildl.Serv., (582):10 p. Also
issued as Fishery Leaflet.U.S.Fish Wildl.Serv., (480)14 p. (1959)
- Johnson, F.F. and M.J. Lindner, Shrimp industry of the South Atlantic and Gulf states.
1934 Investl Rep.U.S.Bur.Fish., 21:83 p.
- Johnson, M.C. and J.R. Fielding, Propagation of the white shrimp, Penaeus setiferus
1956 (Linn.), in captivity. Tulane Stud.Zool., 4(6):173-90

- Jones, D.B., O. Moeller and C.E.F. Gersdorff, The nitrogen distribution and percentages of some amino acids in the muscle of the shrimp, Penaeus setiferus (L). J.biol.Chem., 65(1):59-66
1925
- Joyce, E.A., Jr., The commercial shrimps of the northeast coast of Florida. Prof.Pap. Ser.mar.Lab.Fla., 6:224 p.
1965
- Joyce, E.A., Jr. and B. Eldred, The Florida shrimping industry. Eduo.Ser.Fla St.Bd Conserv., 15:47 p.
1966
- King, J.E., A study of the reproductive organs of the common marine shrimp, Penaeus setiferus (Linnaeus). Biol.Bull.mar.biol.Lab., Woods Hole, 94(3):244-62
1948
- Klima, E.F., Mark-recapture experiments with brown and white shrimp in the northern Gulf of Mexico. Proc.Gulf Caribb.Fish.Inst., 16:52-64
1963
- Knake, B.O., J.F. Murdock and J.P. Cating. Double-rig shrimp trawling in the Gulf of Mexico. Fishery Leafl.U.S.Fish Wildl.Serv., (470):11 p.
1958
- Knapp, F.T., Menhaden utilization in relation to the conservation of food and game fishes of the Texas Gulf coast. Trans.Am.Fish.Soc., 79:137-44
1949
- Kruse, D.N., Parasites of the commercial shrimps, Penaeus aztecus Ives, P. duorarum Burkenroad, and P. setiferus (Linnaeus). Tulane Stud.Zool., 7(4):123-44
1959
- Kutkuhn, J.H., Gulf of Mexico commercial shrimp populations - trends and characteristics, 1956-59. Fishery Bull.U.S.Fish Wildl.Serv., 62(212):343-402
1962
- Leone, C.A. and C.W. Pryor, Serological correspondence among three species of penaeid crustacea. J. Elisha Mitchell scient.Soc., 68(1):27-31
1952
- Lindner, M.J., Estimation of growth rate in animals by marking experiments. Fishery Bull.U.S.Fish Wildl.Serv., 54(78):65-9
1953
- _____, Survey of shrimp fisheries of Central and South America. Spec.scient. Rep.U.S.Fish Wildl.Serv.(Fish.), (235):166 p.
1957
- Lindner, M.J. and W.W. Anderson, Growth, migration, spawning and size distribution of shrimp Penaeus setiferus. Fishery Bull.U.S.Fish Wildl.Serv., 56(106):555-645
1956
- Loesch, H., Distribution and growth of penaeid shrimp in Mobile Bay, Alabama. Publ Inst.mar.Sci.Univ.Tex., 10:41-58
1965
- Love, T.D. and M.H. Thompson, Annual report Bureau of Commercial Fisheries Technological Laboratory, Pascagoula, Mississippi, Fiscal Year 1965. Circ. Fish Wildl.Serv., Wash., (251):25 p.
1966
- Lunz, G.R., Harvest from an experimental one-acre salt-water pond at Bears Bluff Laboratories, South Carolina. Progre Fish Cult, 18:92-4
1956
- _____, Pond cultivation of shrimp in South Carolina. Proc.Gulf Caribb.Fish. Inst., 10:44-8
1958
- _____, Annual report 1965-1966. Bears Bluff Laboratories, Wadmalaw Island, South Carolina. Contr.Bears Bluff Labs., 44:11 p.
1967
- Lunz, G.R. and C.M. Bearden, Control of predaceous fishes in shrimp farming in South Carolina. Contr.Bears Bluff Labs., 36:9 p.
1963
- McFarland, W.N. and B.D. Lee, Osmotic and ionic concentrations of penaeidean shrimps of the Texas coast. Bull.mar.Sci.Gulf Caribb., 13(3):391-417
1963

- Moock, C.R., Natural and altered estuarine habitats. Galveston, Texas, Bureau of
MS Commercial Fisheries Biological Laboratory, 18 p.
- Olivier, G.A., Écrevisse. Astacus. In Encyclopédie méthodique. Histoire naturelle.
1791 Insectes. Paris, Vol.6:327-49
- Pearson, J.C., The early life histories of some American Penaeidae, chiefly the com-
1939 mercial shrimp, *Penaeus setiferus* (Linn.). Bull.Bur.Fish., Wash., 49(3):73 p.
- Pérez-Farfante, I., Western Atlantic shrimps of the genus *Penaeus*. Fish.Bull.U.S.Fish
1969 Wildl.Serv., 67(3):461-591
- _____, Sinopsis de datos biológicos sobre el camarón blanco *Penaeus schmitti*
1970 Burkenroad, 1936. FAO Fish.Rep., (57) Vol.4:1417-38
- Power, E.A., Fishery statistics of the United States, 1958. Statist.Dig.U.S.Fish Wildl.
1960 Serv., 43:424 p.
- Renfro, W.C. and H.A. Brusher, Seasonal abundance, size distribution, and spawning of
MS penaeid shrimp in the northwestern Gulf of Mexico.
- Rioja, E., Estudios carcinológicos. 1. Caracteres sexuales secundarios de los
1939 Penaeidae - El órgano antennular de los machos. An.Inst.Biol.Univ.Méx.,
10:313-9
- _____, Estudios carcinológicos. 4. Observaciones sobre las antenulas de al-
1940 gunas especies del género *Penaeus*. An.Inst.Biol.Univ.Méx., 11:267-73
- _____, Estudios carcinológicos. 8. Contribución a la morfología e inter-
1941 pretación del petasma de los Penaeidae (Crust. Decapodos). An.Inst.Biol.Univ.
Méx., 12:199-221
- _____, Estudios carcinológicos. 20. Valor diagnóstico del tercer maxilipedo
1948 y de sus cerdas en algunas especies del género *Penaeus* de la costa de
México. An.Inst.Biol.Univ.Méx., 19:453-67
- Robas, J.S., Shrimp trawling gear as used in the Gulf of Mexico. In Modern fishing
1959 gear of the world, edited by H. Kristjonsson. London, Fishing News (Books)
Ltd., pp. 311-6
- Say, T., An account of the Crustacea of the United States. J.Acad.nat.Sci.Philad. 1:
1818 235-53
- Seba, A., Locupletissimi rerum naturalium thesauri accurata descriptio, et iconibus
1759 artificiosissimis expressio, per universam physices historiam. Amstelædami,
H.D. Gaubius, Vol.3, 212 p.
- Simmons, E.G., An ecological survey of upper Laguna Madre of Texas. Publs Inst.mar.
1957 Sci.Univ.Tex., 4(2):156-200
- Sprague, V., Notes on three microsporidian parasites of decapod crustacea of Louisiana
1950 coastal waters. Occ.Pap.mar.Lab.La St.Univ., (5):1-8
- _____, Protozoa. In Gulf of Mexico, its origin, waters and marine life.
1954 Fishery Bull.U.S.Fish Wildl.Serv., 55(89):243-56
- Springer, S. and H.B. Bullis, Exploratory shrimp fishing in the Gulf of Mexico, 1950-
1952 51. Fishery Leaflet.U.S.Fish Wildl.Serv., (406):34 p.
- Temple, R.F. and C.C. Fisher, Vertical distribution of the planktonic stages of penaeid
1965 shrimp. Publs Inst.mar.Sci.Univ.Tex., 10:59-67